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Recent invasion of Ponto-Caspian amphipods in the Masurian Lakeland associated with human leisure activities

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Abstract

Non-indigenous species (NIS) contribute to the decrease of native species' diversity on a local and global scale. One of Europe's most significant donors of freshwater invasions is the Ponto-Caspian Region. Following the construction of artificial canals connecting isolated waterbodies and the resulting heavy boat traffic, the Ponto-Caspian Amphipoda started to spread in Europe. Four amphipod species: *Dikerogammarus haemobaphes*, *Dikerogammarus villosus*, *Pontogammarus robustoides* and *Chaetogammarus ischnus* have invaded the Masurian Lakeland (North-eastern Poland). Based on literature and our data, we studied their distribution in 22 lakes in the region during the years 2001–2016. We analysed their distribution against several water quality parameters and levels of anthropogenic pressure. Our results also present the first records of two new invaders, *D. villosus* and *C. ischnus*, in the studied area. We show that the relative abundance and frequency of these two species rapidly increase and, simultaneously, the populations of the earlier invaders, i.e. *D. haemobaphes* and *P. robustoides*, decrease. The native species – *Gammarus lacustris* – seems to be negatively affected by NIS richness, as well as by the proximity of towns. The spread of NIS in the lakes appears to be facilitated by boating and the lower complexity of the shoreline. Our study shows how anthropogenic pressure, especially tourism, can facilitate bioinvasion, jeopardising native biodiversity unless appropriate regulations are implemented.

Keywords

assemblage succession, biological invasions, lakes, propagule pressure, recreational boating, time series, tourist pressure

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Introduction

Biological invasions are perceived as the second strongest threat to biodiversity on a local and global scale, right after habitat degradation (e.g. CBD (2000); Sala et al. (2000); Dudgeon et al. (2006); Kettunen et al. (2009); Strayer and Dudgeon (2010); Lambertini et al. (2011); Mačić et al. (2018); Lipták et al. (2019); Iqbal et al. (2021); Yang et al. (2021); Vantarová et al. (2023)). Many non-indigenous species (NIS) cause declines in abundance and diversity of native species, which is particularly apparent in Europe and the USA (e.g. Pinkster et al. (1992); Dick and Platvoet (1996, 2000); Ricciardi and MacIsaac (2000); Ricciardi (2006); Bellard et al. (2016); Panlasigui et al. (2018); Albano et al. (2021); Haubrock et al. (2021); Yang et al. (2021)) and is more prominent in freshwater ecosystems than in marine and terrestrial ones (Strayer and Dudgeon 2010). Many studies show high economic costs incurred by biological invasions on a global scale (Pyšek and Richardson 2010; Cuthbert et al. 2021a, b; Kouba et al. 2022). The average annual costs of preventing biological invasions and reversing their effects globally reach $76 billion (Bradshaw et al. 2016); however, the costs of prevention of invasion are much lower than post-invasion management (Cuthbert et al. 2021a). Globally, the economic costs of aquatic bioinvasions have been estimated at $23 billion (Cuthbert et al. 2021b). The costs of amphipod invasions constitute a small part of the global costs of aquatic crustacean invasions ($180,000 out of an estimated $271 million); however, these costs are underestimated (Kouba et al. 2022).

Even though surface freshwaters represent only 0.01% of the Earth's water resources and constitute 0.80% of the Earth's surface, they are inhabited by ca. 6% of the world's species (Dudgeon et al. 2006; Strayer and Dudgeon 2010). Therefore, freshwater ecosystems are precious from environmental, economic, sanitary, cultural and scientific perspectives and also constitute a valuable spot for tourism (Dudgeon et al. 2006; Hall and Härkönen 2006). Unfortunately, these ecosystems are in crisis, as indicated by stronger biodiversity loss than in terrestrial ecosystems (Dudgeon et al. 2006). According to the Water Framework Directive (European Environment Agency 2000), every waterbody in the EU should have achieved a high or at least good ecological and chemical status by 2015. However, the latest reports indicate that only 40% of such waters have achieved a satisfactory, healthy status (European Environment Agency 2018). Land use and agriculture are amongst the most important factors in aquatic ecosystems' declining conditions globally (Foley et al. 2005; Feld et al. 2016). Thus, although freshwater ecosystems constitute only a tiny fraction of the Earth's surface, high anthropogenic pressure results in a more pronounced negative impact of invaders on native species than in marine ecosystems (Ricciardi and Kipp 2008).

One of the richest European sources of species invading inland waters is the Ponto-Caspian Region (Ricciardi and MacIsaac 2000; Bij de Vaate et al. 2002; Galil et al. 2008; Panov et al. 2009; Copilaș-Ciocianu et al. 2023a). This region covers the coastal area of the Caspian, Black, Aral and Azov Seas, with their brackish limans and deltas of rivers discharging into these seas (Jażdżewski 1980). The Ponto-Caspian basin constitutes a hotspot of crustacean diversity, particularly in the case of amphi-

pod crustaceans (Cristescu and Hebert 2005; Väinölä et al. 2008; Copilaș-Ciocianu and Sidorov 2022; Copilaș-Ciocianu et al. 2022). Ponto-Caspian amphipods comprise around 10% of European freshwater invasive species (Pöckl et al. 2011). One of the main significant causes fuelling the bioinvasions of Ponto-Caspian species is the construction of canals that connect previously isolated watersheds (e.g. Jażdżewski (1980); Bij de Vaate et al. (2002); Nehring (2005); Galil et al. (2008); Arbačiauskas et al. (2010); Minchin et al. (2019); Jażdżewska et al. (2020)). Another important factor is translocations of species in ballast waters (Jażdżewski 1980; Pinkster et al. 1992; Bij de Vaate et al. 2002; Zhulidov et al. 2018). However, a more important vector of bioinvasions in freshwater ecosystems is transporting on biofouled hulls, filters and other submerged parts of vessels (Nehring 2005; Hewitt et al. 2009; Bącela-Spychalska et al. 2013; Anderson et al. 2014, 2015; De Ventura et al. 2016; Rewicz et al. 2017; Rodríguez-Rey et al. 2021). Biofouling of vessels by species resistant to desiccation enables their subsequent overland transport and the colonisation of isolated waterbodies (Bącela-Spychalska et al. 2013; Rachalewski et al. 2013; De Ventura et al. 2016). Fishing and diving equipment can also be an effective vector of invasions (Bącela-Spychalska et al. 2013; Anderson et al. 2014; Smith et al. 2020). Moreover, many species are also intentionally introduced into freshwater ecosystems (Grigorovich et al. 2002; Nehring 2005).

Seven species of Ponto-Caspian gammarids (Amphipoda, Gammaroidea) have already been recorded from Polish freshwaters: *Chaetogammarus ischnus* (Stebbing, 1899), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Dikerogammarus villosus* (Sowinsky, 1894), *Obesogammarus crassus* (G.O. Sars, 1894), *Pontogammarus robustoides* (Sars, 1894), *Spirogammarus major* (Cărăușu, 1943) (former European population of *Echinogammarus trichiatus*) and *Chelicorophium curvispinum* (G.O. Sars, 1895) (Konopacka 1998; Gruszka 1999; Jażdżewski and Konopacka 2000; Konopacka and Jażdżewski 2002; Jażdżewski et al. 2005; Grabowski et al. 2007; Rachalewski et al. 2013; Copilaș-Ciocianu et al. 2023b). These species are already widely distributed in European inland waters, where they arrived through well-defined migration corridors: northern, central and southern (Bij de Vaate et al. 2002; Panov et al. 2009). Not only have they colonised the major rivers and canals constituting the invasions corridors, but also spread to the watersheds of these rivers, as well as many European lakes, for example, the Alpine Lakes (Rewicz et al. 2017) and the Great Masurian Lakes in Poland (Jażdżewski 2003; Jażdżewska and Jażdżewski 2008). An extensive up-to-date description of the distribution of alien freshwater amphipods in Europe can be found in Copilaș-Ciocianu et al. (2023a). As the dynamics of invasion in terms of species and ecosystem vulnerability varies and the impact of NIS depends on their invasion process (i.e. propagule pressure, species interactions), there is a constant need for monitoring and estimating trends and threats regarding invasions. The impact of invasive species on aquatic ecosystems is profound (Kurashov et al. 2012). Their introduction may lead to drastic changes in the macroinvertebrate community structure and affect the functioning of whole ecosystems (Jones et al. 1994; Jones et al. 1997; Lambertini et al. 2011). NIS can modify habitats as well as food chains and contribute to changes in

energy flows – benthic communities can be transformed from being energy suppliers to upper trophic levels becoming major consumers of ecosystem energy (Nalepa et al. 2009; Kurashov et al. 2012).

Lakes seem to be particularly susceptible to biological invasions, as many of them are under high tourist pressure, resulting in a higher probability of alien species introduction, even if the lakes are not directly connected with the invasion corridor (Bącela-Spychalska et al. 2013; Bącela-Spychalska 2016; De Ventura et al. 2016; Rewicz et al. 2017). One such region is the Masurian Lakeland. It is the most popular area for yachting in Poland and one of central Europe's main inland yachting regions. The region is extensively used for associated recreational activities, particularly angling and camping (Kistowski and Śleszyński 2010; Ulikowski et al. 2021). Unfortunately, the level of knowledge about the risks of spreading invasive Amphipoda in this region is poor and out of date (Jażdżewski 2003; Jażdżewska and Jażdżewski 2008). Previous studies were based on sampling from only a few lakes, provided mainly presence/absence data and predated the effect of increased recreational pressure. Knowledge about the role of tourism, shipping and other factors in biological invasions in the Masurian Lakeland is poor and demands study. Given the significance of these factors in other regions, it is likely that their influence in the Masurian Lakeland is also considerable. The intensity of shipping and, therefore, its effect on biological invasions will increase with time (Sardain et al. 2019). Thus, it is crucial to understand these mechanisms in the study area. We also do not know how the invasion of amphipods affected native amphipods in the region. With regards to the faunistic data about the native amphipod species in the Lakeland, Jażdżewski and Konopacka (1995) mention two widely distributed lacustrine species, namely *Gammarus lacustris* G.O. Sars, 1863 and *Pallasiola quadrispinosa* (G.O. Sars, 1867). However, these data are old and require updating.

The aims of our study were: i) to update the knowledge on the distribution and expansion of the Ponto-Caspian amphipod fauna in the Masurian Lakeland; ii) to assess the distribution of native vs. invasive Ponto-Caspian amphipods in the context of biotic and abiotic characteristics of the lakes and anthropogenic pressure in this region, using both historical and newly-obtained data. Based on observed trends in other regions (e.g. Dick and Platvoet (2000); Grabowski et al. (2006); Van der Velde et al. (2009); Meßner and Zettler (2021)), we assumed that some invasive amphipods are replaced by stronger competitors and that native species are not able to co-exist with the invasive species. We hypothesise that high tourist pressure contributes to the dispersion of invasive amphipods, while the occurrence of the native species is linked to isolated lakes.

We tracked the distribution of invasive Amphipoda in the Masurian Lakeland since 2001, based on literature and our data. To explore the relationship between the structure of amphipod assemblages and lake characteristics, including human tourist pressure in the years 2014 and 2016, we collected data on the relative abundance of amphipods, measured basic water parameters, implemented hydromorphological data and estimated the tourist pressure.

Materials and methods

Study area

The Masurian Lakeland (Pojezierze Mazurskie in Polish) is a lake district (macroregion) in North-eastern Poland with a surface area of 52,000 km^2 including seven mesoregions, amongst others, the Land of the Great Masurian Lakes (Kraina Wielkich Jezior Mazurskich in Polish) and the Ełckie Lakeland (Pojezierze Ełckie in Polish) (Kondracki 2002). The landscape was formed between 16,000 and 11,000 BP (at the end of the last glaciation) and is characterised by strong latitude differentiation, dominantly with moraine hills (Hillbricht-Ilkowska et al. 2000; Ulikowski et al. 2021) and with glacial tills as a dominant component of the soil substratum (Hillbricht-Ilkowska et al. 2000). The lakes are mainly surrounded by a mosaic of agricultural areas and forests giving similar input of allochthonous organic and mineral matter to each lake (Chróst and Siuda 2006; Ejsmont-Karabin et al. 2020). Most lakes of this region are dimictic with summer thermal stratification (Ulikowski et al. 2021). They are connected with main European watersheds via artificial canals and small rivers: the River Pisa (flowing into the River Narew and then into the River Vistula) and the River Węgorapa (flowing into the River Pregolya and then into the Vistula Lagoon) (Bajkiewicz-Grabowska 2008; Jażdżewska and Jażdżewski 2008; Ulikowski et al. 2021). This connectivity increases the probability of invasive amphipods spreading in the region. For this study, we selected lakes with historical faunistic data, based on Jażdżewski and Konopacka (1995), as well as along a gradient of tourist pressure, including more natural and isolated lakes. We also selected sampling points on the rivers, i.e. the River Węgorapa, the River Pisa and the River Narew, which connect the Masurian Lakeland with major rivers, for example, the River Vistula and the River Neman (Fig. 1; see also Suppl. material 1).

Sampling and data collection

Our dataset consists of two types of data: (*i*) published, including the years between 2001 and 2007 (Jażdżewski 2003; Jażdżewska and Jażdżewski 2008) and (*ii*) new data coming from field surveys in 2008, 2009, 2014 and 2016. Additionally, to facilitate the monitoring of the amphipod expansion and to model the distribution of native *Gammarus lacustris*, we incorporated records from several lakes and the River Narew, which are situated outside of the study area (see Suppl. material 1). The studies that were conducted between 2001 and 2009 only have a qualitative character (i.e. presence/absence of amphipod species), while for 2014 and 2016, the species abundances are available. Generally, sampling was done through "kick-sampling" with a benthic hand-net with a mesh size of 0.5 mm, used for 45 min at each station, performed by two people with equal effort, from all available littoral habitats (sand, mud, gravel, stones and submerged macrophytes) at depths from 0.05 to 0.5 m. Such a semi-quantitative method gives reliable and comparable results for all sampling points and all study years/periods (Jażdżewski et al. 2002; Grabowski et al. 2006). The amphipods

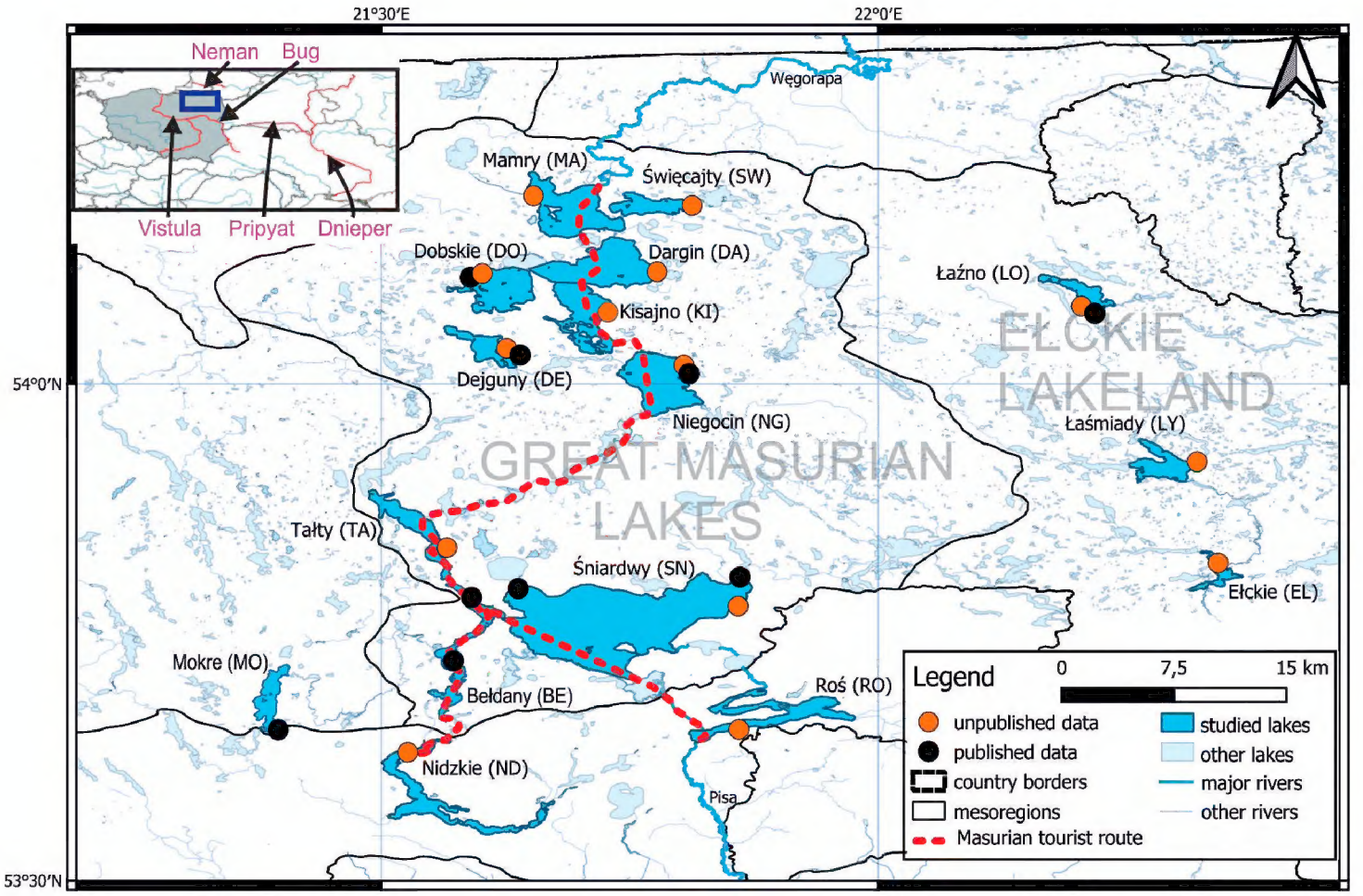

Figure 1. The sites in the Masurian Lakeland. Sites were divided into previously unpublished (records of this study) and published (Jażdżewski 2003; Jażdżewska and Jażdżewski 2008). Mesoregions are delimited according to Kondracki (2002). The two-letter acronyms for particular lakes were used in further Figures and Suppl. material 1.

were preserved in 96% ethanol and then identified in the laboratory to the species level, based on the available literature (Mordukhai-Boltovskoi 1964; Eggers and Martens 2001). This collection and preservation protocol was used at all studied sites and in all study years.

To detect the potential role of biotic and abiotic factors, as well as human pressure on the presence of invasive amphipods in the lakes sampled in 2014 and 2016, we used topological and anthropogenic variables, such as the surface-volume ratio or the distance from town. As a proxy of the level of anthropogenic pressure, we used the water quality status (water QS) from Soszka et al. (2016). This index categorises the waterbodies into six water quality categories (ranging from excellent – class I, to very poor – class VI), based on species assemblages and chemical and physical parameters of water according to the Water Framework Directive (European Environment Agency 2000). We presume that lower values of this variable (lower water class), indicating increased species diversity and reduced levels of nutrients and heavy metals in the water (better water quality), correspond to lower levels of anthropogenic pressure on the lake (European Environment Agency 2000; Sánchez et al. 2007; Lobato et al. 2015). Environmental heterogeneity creates more niches that can be occupied by co-occurring species (Chesson 2000). Thus, we used two indices: shoreline development (shoreline length to surface area ratio) from mojemazury.pl and surface

area to volume ratio (A/V ratio) from Soszka et al. (2016). The shoreline development index is the ratio of the actual shoreline length of a lake to the circumference of a perfectly circular lake with the same area (Aronow 1982). High values indicate a more complex shoreline, retaining a higher load of nutrients from land (Cole 1975) and providing more niches for the biota (Chesson 2000). The surface area to volume ratio combines information about the depth and size of the lake and can be positively correlated with the productivity of the lake (Fee 1979). Smaller waterbodies (lower A/V ratio) may play the role of refugia for native species (Grabowski et al. 2009). The density of boats (i.e. the number of boats divided by the lake surface in ha), was obtained as the maximum possible number of moored boats in marinas (Johnson and Padilla 1996; Vander Zanden and Olden 2008; Ros et al. 2013). We assumed that the higher the density of boats in the lakes, the higher the tourist pressure and the higher the probability of transport of invasive species by vessels (Johnson and Padilla 1996; Vander Zanden and Olden 2008; Bącela-Spychalska et al. 2013; Ros et al. 2013). The maximum capacity of marinas was obtained from websites: mazury24.eu and skorupki.mazury.info.pl. Tourist infrastructure is mainly localised in urban areas (Kulczyk et al. 2016). Thus, we used the distance between the sampling point and towns (i.e. centroid) as an estimation of anthropogenic pressure. Moreover, land use in the vicinity of water-bodies can impact the temporal variations in amphipod assemblages (Cereghetti 2023). The distance was measured as a linear distance in km from the centroid of the closest town to the sampling point using QGIS software. Towns were designated according to the ESRI shapefile "UIA World Countries Boundaries", available at: https://hub.arcgis.com/datasets/UIA::uia-world-countries-boundaries. All spatial analyses and their visualisation were conducted using QGIS 3.10.13 (QGIS Development Team 2020).

Data analysis

Using all unpublished records since 2008 from the lakes and the rivers, including sites outside the study area (see Suppl. material 1), we modelled the presence of the only native gammarid (i.e. *Gammarus lacustris*) according to the number of NIS and the relative distance of each sampling site from town. We included this variable as a proxy of the anthropogenic propagule pressure (i.e. the introduction of NIS by human activities) of NIS at each site (i.e. inversely correlated). We used generalised linear mixed models (GLMMs) to include the random variable of the sampling year. Given the presence/absence nature of the data, we used a Bernoulli distribution fitted with glmmTMB (link = logit) with the homonymous package (Brooks et al. 2017). The possible inclusion of the interaction between NIS richness (i.e. number of species) and the distance from the closest town was also tested using the Akaike Information Criterion (AIC; Bozdogan (1987)). After fitting the model, we validated it by simulating its residuals using the package DHARMa (Hartig 2022). We also confirmed the absence of spatial autocorrelation of the residuals using the Spatial Autocorrelation function of the DHARMa package.

Using samples collected in 2014 and 2016, we first explored the variability of the environmental parameters of the sites and lakes, grouping them according to their geographical position and connectivity (i.e. I: northern, II: southern, III: eastern; Fig. 2B, see also Suppl. material 1). We hypothesised that nearby and interconnected lakes would exhibit comparable gammarid assemblages. This assumption is supported by findings from the Great Lakes in the USA, where the likelihood of species invasion was found to be the highest near the mouth of canals connecting the lakes (Grigorovich et al. 2005). To explore and visualise the environmental variability of the study area, we used a principal component analysis (PCA) with standardised values with *prcomp* of the package vegan (Oksanen et al. 2022). We analysed the gammarid assemblage using a permutational multivariate analysis of the covariance (PERMANCOVA) with an orthogonal design with two fixed factors (i.e. lake groups with three levels – I, II, III; time with two levels – 2014 and 2016) and five covariates: water QS, A/V ratio, shoreline development, density of boats and distance from the town. To control the possible sampling differences (i.e. being semi-quantitative), Hellinger distances were used to compare the abundances of the different species. To account for the excess of zero values, a dummy variable of 0.0001 was added to the whole dataset. We used first adonis2 of the package vegan with 9999 permutations and pairwise.adonis of the package pairwiseAdonis, with Holm correction and 9999 permutations, for the post hoc analysis between levels of the significant factors (Martinez Arbizu 2020). To visualise and corroborate the results of the PERMANCOVA, we finally used a constrained ordination using distance-based redundancy analysis (dbRDA), based on Legendre and Anderson (1999), with capscale (package vegan) and Hellinger distances, as for Permancova, including the covariates of the PERMANCOVA as constraining variables. All the analyses were performed in the R environment 4.3.0 version (R Core Team 2023).

Results

Temporal and spatial distribution of invasive species

We recorded four invasive gammarid species from 12 lakes and the Rivers Węgorapa and Pisa and one native species (*Gammarus lacustris*) from 16 lakes (Fig. 2A, Suppl. material 1). The first recorded invasive species was *Dikerogammarus haemobaphes* found in 2001 (Jażdżewski 2003) and the second was *Pontogammarus robustoides*, which was first observed in 2007 (Jażdżewska and Jażdżewski 2008). The spread of invasive species can be observed over time (Fig. 2B). Between 2014 and 2016, *D. haemobaphes* spread to one more lake and is observed now in nine of them. *Pontogammarus robustoides* did not colonise new lakes in 2016, compared to 2014. In 2014, we noticed the first appearance of the other two invaders: *C. ischnus* and *D. villosus* (Fig. 2A). The previous species was found in two lakes in 2014 and expanded to five further lakes in 2016, while the latter one was already found in five lakes in 2014 and expanded to two further lakes in 2016 (Fig. 2A). Although *Chaetogammarus ischnus* was recorded in the River Pisa in 2014 and 2016, *D. villosus* was not found in any of the studied rivers

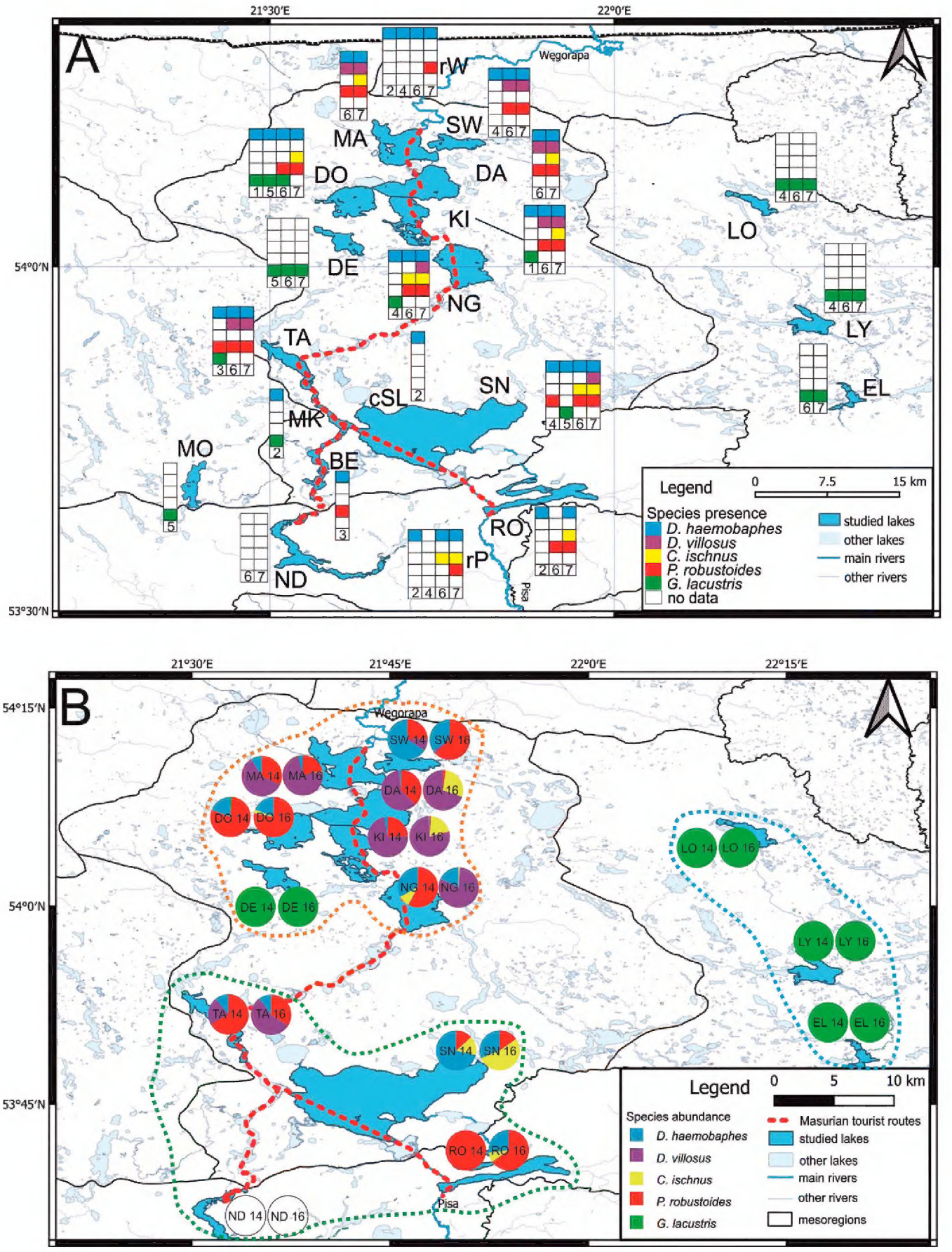

Figure 2. A the distribution of invasive and native amphipod species in studied lakes since 2001, based on published and new data (locality codes according to Suppl. material 1). Table at each lake showing the assemblage (colours in rectangles according to different species, see legend) variation in time (symbols for sampling years: 1 – 2001; 2 – 2002; 3 – 2007; 4 – 2008; 5 – 2009; 6 – 2014; 7 – 2016). Only years of samplings from each lake and river are shown. Colourless rectangles indicate that no amphipods were recorded during the sampling. The dashed black line indicates country borders; the dashed red line indicates the Masurian tourist boat route. Black lines delimit mesoregions according to Kondracki (2002) **B** the assemblage composition of the amphipod fauna in studied lakes in the years 2014 and 2016 (locality codes according to Suppl. material 1). Pie charts show the relative abundances of each species. An empty circle means no amphipods were recorded. Black lines delimit mesoregions according to Kondracki (2002). Coloured dotted lines around the pie charts correspond to the lake groups: orange – I, green – II, blue – III.

(Fig. 2A) The relative abundance of new invaders (*D. villosus* and *C. ischnus*) increased with time, while it decreased for *D. haemobaphes* and *P. robustoides* (Fig. 2B). In Lake Nidzkie, we did not record any amphipod species (Fig. 2A, B).

The modelled occurrence of native *Gammarus lacustris*

Generally, the native species – *Gammarus lacustris* – was not found in lakes inhabited by invasive species, apart from Lake Dobskie, where the native and invasive gammarids co-occurred in 2014 with a low number of *G. lacustris* (two individuals vs. 194 individuals of invasive species) (Fig. 2A, B; Suppl. material 1). The GLMM for the presence of *G. lacustris* showed the significant negative effect of NIS richness (p-value = 0.002) and the positive effect of the distance from town (p-value = 0.024), but not their interaction (Fig. 3). The inclusion of the year as a random effect barely increased the R^2 (Marginal 0.733 – Conditional 0.808), supporting the effectiveness in sampling efforts (Suppl. materials 2, 4).

Environmental factors and amphipod assemblage

The first three components of the PCA explained 85.5% of the variance amongst the environmental variables (Fig. 4A, B). According to PC1 and PC3 (~ 57% variance explained), the lakes further from the tourist route (i.e. group III) are, indeed, characterised by a lower number of boats, higher complexity of the shore and a greater distance from town. The PC2 was more related to the water quality status (water class) and the surface-volume ratio showing a general trend of better water quality (lower class of water quality status) and deeper waters for group I (highest class of water status – lowest water quality for group II). The PERMANCOVA results showed significant effects (p-values < 0.05) of shoreline development ($F = 22.096$, $p < 0.001$), the number of boats ($F = 10.788$, $p < 0.001$) and water quality status – water class ($F = 3.794$, $p = 0.035$) on the assemblage of amphipods (Suppl. material 3). Even though the relative abundance of species changed with time, i.e. increased in *D. villosus* and *C. ischnus* and decreased

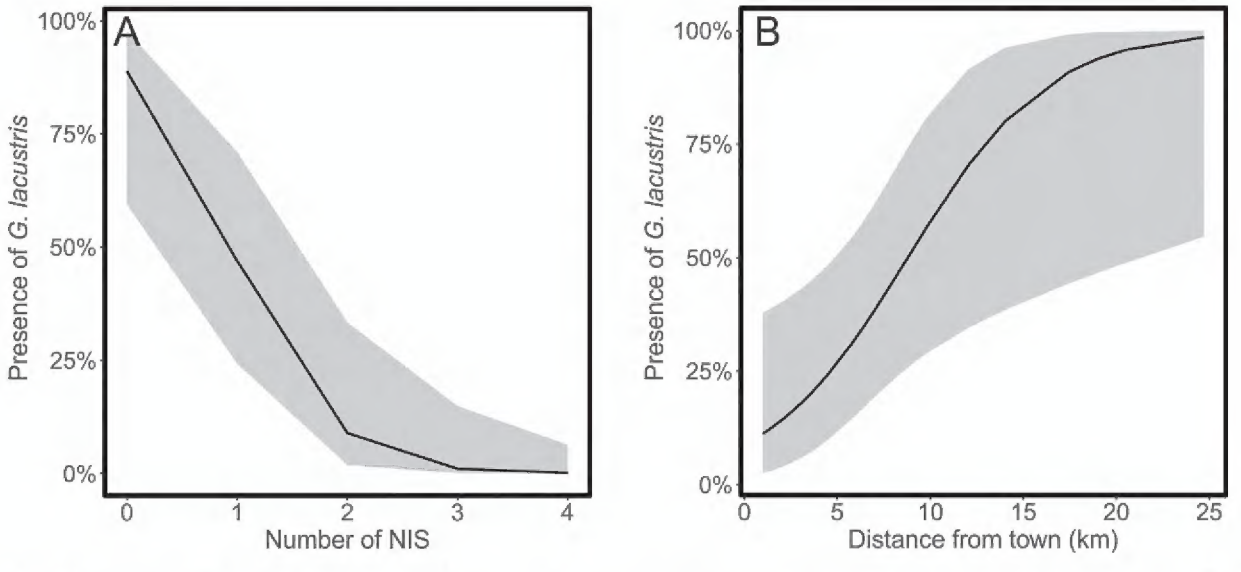

Figure 3. The predicted probability of occurrence of *G. lacustris* dependent on the richness of NIS (A) and the distance of the sampling point from town (B). The grey area delimits the 95% confidence intervals.

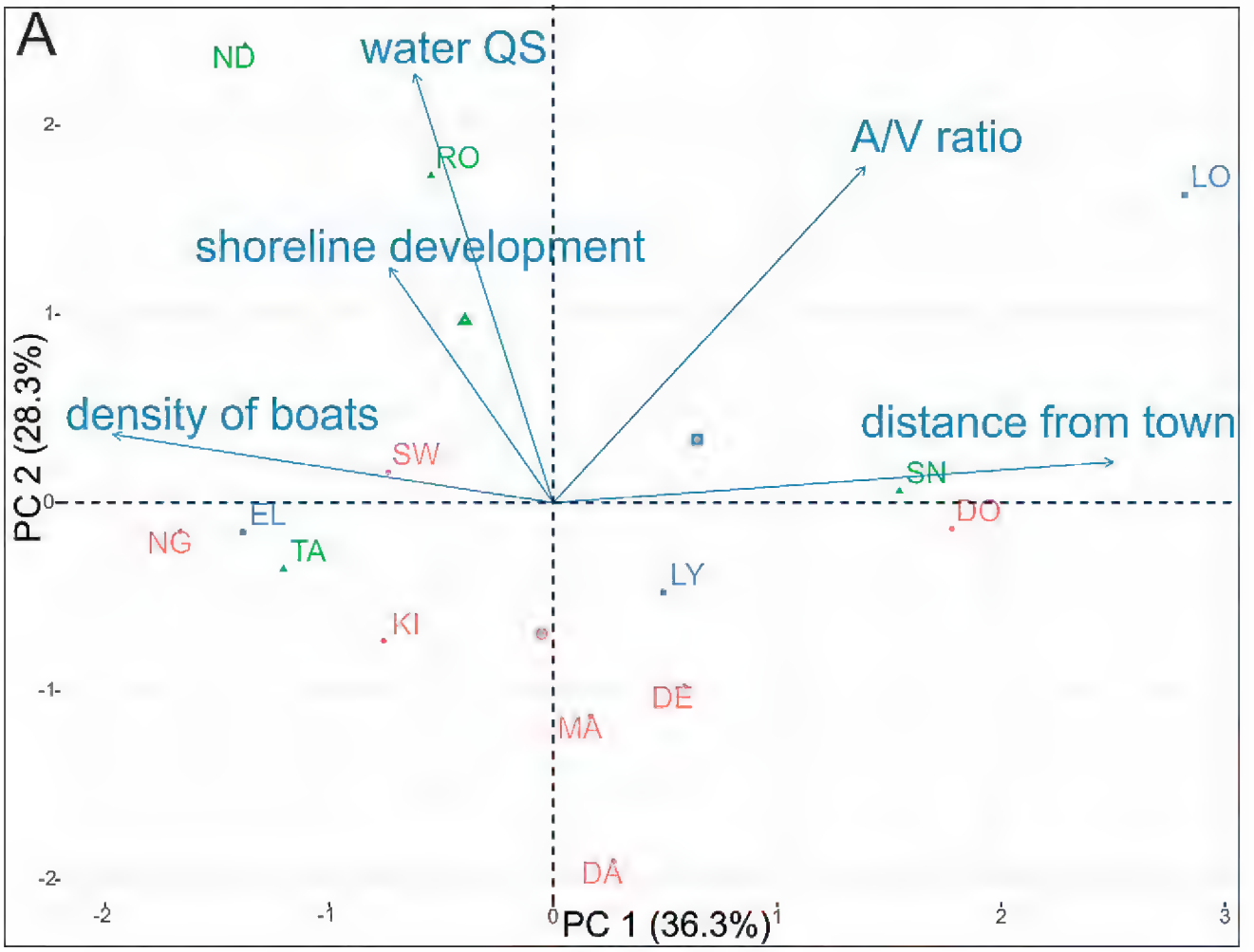

Figure 4. Biplots displaying the first three axes of the PCA of the environmental variables of the lakes sampled in 2014 and 2016 (**A** PC1-2 **B** PC1-3). The colours refer to the different lake groups: orange circles (I), green triangles (II) and blue squares (III). The lengths of the arrows are proportional to the loading of each variable, dashed lines = 0. The acronyms of lakes are according to Fig. 1 and Suppl. material 1.

in *D. haemobaphes*, *P. robustoides* and *G. lacustris*, the time factor was not significant. The differences in amphipod assemblages between lake groups (determined, based on the geographical position and interconnections between the lakes) were marginally significant, i.e. F = 2.680, p = 0.057) and the post hoc analysis showed a significant difference (p.adjusted < 0.001) between the group III (i.e. eastern group) and the others, but not between the first two (p.adjusted > 0.4).

The first two axes of the dbRDA fitted 90.1% of 52.1% of the total variation explained (Fig. 5). The presence of the native *G. lacustris* appeared more correlated to lakes with more complex shorelines. The occurrence of *D. villosus* was mainly explained by the increasing number of boats and proximity to town. The other three species (i.e. *P. robustoides*, *D. haemobaphes* and *C. ischnus*) seemed to be related to simpler shorelines and average values for the other variables, which was generally the opposite to *D. villosus*.

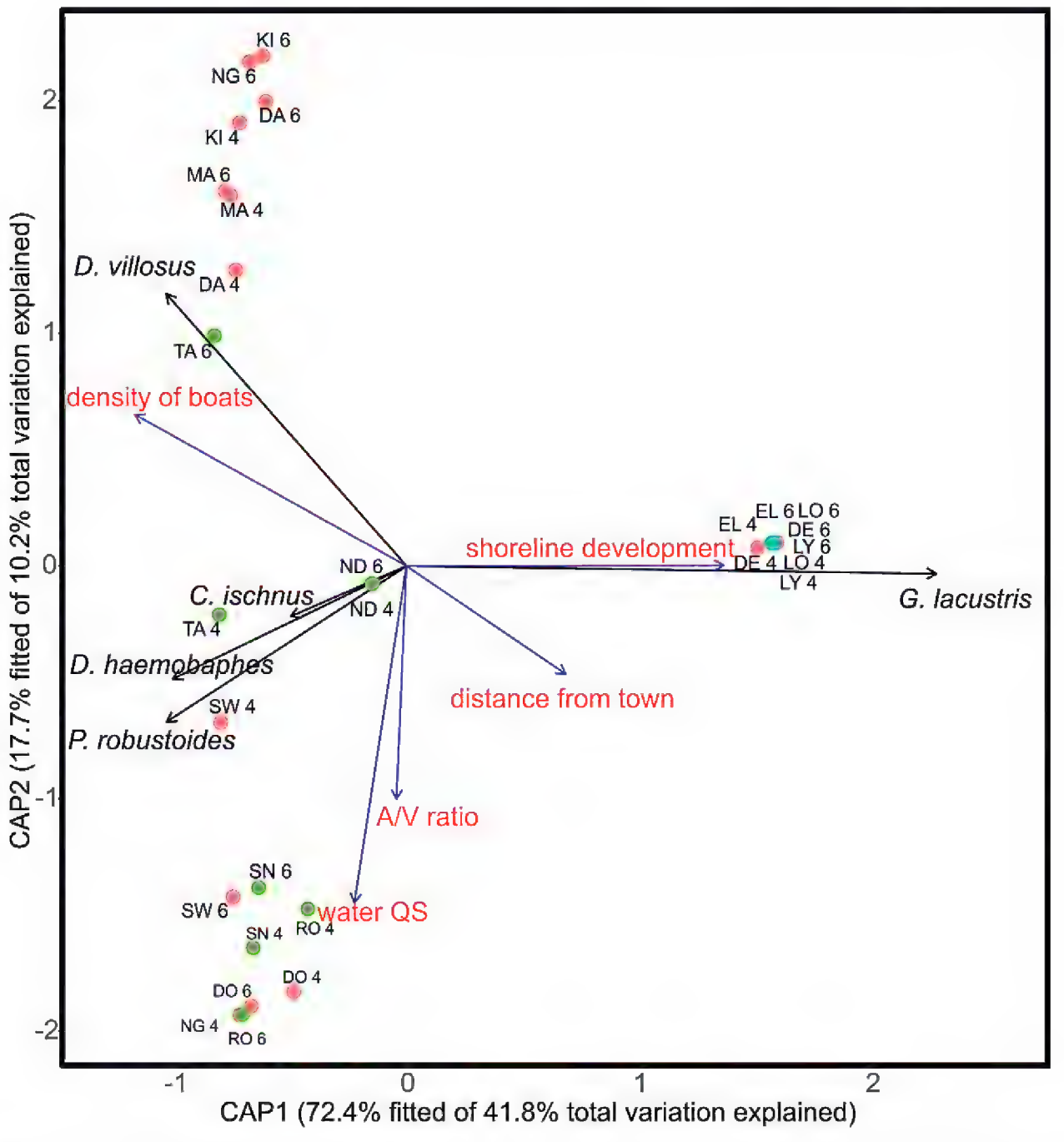

Figure 5. Canonical analysis of principal coordinates (CAPSCALE) derived from the Bray-Curtis dissimilarities of the gammarid assemblages and the environmental variables of the studied lakes in the years 2014 and 2016. The colours of the dots refer to the different lake groups: orange circles (I), green circles (II) and blue circles (III).

Discussion

Our study shows that, between 2001 and 2016, the number of invasive amphipod species in the study area increased drastically from one (*D. haemobaphes*) to four (three more species recorded: *D. villosus*, *P. robustoides*, *C. ischnus*). Simultaneously, a continuous decrease in the occurrence of native *Gammarus lacustris* was recorded. Our study reveals that the presence of NIS in lakes is primarily facilitated by three key factors: recreational boating activities, proximity to urban areas and simplified lake shorelines.

Distribution of *Gammarus lacustris*

According to our results, the presence of more than one NIS significantly affects the presence of the native *G. lacustris*, bringing the probability of its presence almost to zero already with three NIS (Fig. 3A). The species disappeared several years after the expansion of invasive amphipod species in several lakes (Fig. 2A, Suppl. material 1). For instance, the species was widely distributed until the last record in 2001 in Lake Kisajno (Jażdżewski 2003), in 2007 in Lake Tałty (Jażdżewska and Jażdżewski 2008), in 2008 in Lake Niegocin and in 2009 in Lake Śniardwy. Older data mention the presence of *Gammarus lacustris* in Lake Mamry (Jażdżewski 1975). In these lakes, the disappearance of *G. lacustris* coincided with the invasion of alien species. In 2014, *G. lacustris* was co-occurring with invasive species in only one lake (Lake Dobskie). One potential explanation could be the limited tourist activity in Lake Dobskie, as well as low species introduction probabilities, resulting from the absence of direct connections between this lake and other lakes situated along the Masurian tourist routes. Moreover, in 2014, the invasion of *C. ischnus* and *P. robustoides* in Lake Dobskie was still in its early stage. However, in 2014 the abundance of *G. lacustris* in this lake was very low and we did not record this species in 2016. Additionally, in 2002, we recorded the species co-occurring with *D. haemobaphes* in Lake Mikołajskie, but the presence of *G. lacustris* in this lake in subsequent years is unknown. In general, most of the records of *G. lacustris* in the Masurian Lakeland come from isolated lakes where invasive amphipods did not spread. In 2016, we found this species only in four isolated lakes, i.e. Dejguny, Ełckie, Łaśmiady and Łaźno (Fig. 2A; Suppl. material 1).

These four lakes (three of them in the eastern group of lakes) are characterised by low tourist pressure (low number of boats, long distance from the tourist routes) (Fig. 5). The low level of tourist pressure in these lakes and lack of direct connections with the Great Masurian Lakes (central part of the Masurian Lakeland), where all the invasive amphipods are present, may create a refuge for native species. Furthermore, we found that *G. lacustris* is associated with lakes distanced from towns (Figs 3B, 5). The proximity of the lakes to the urban areas results in their pollution and declining quality of water (Mishra et al. 2023). Although *G. lacustris* has a broad tolerance to environmental factors (Matafonov and Bazova 2014), its populations decline in polluted water, for example, with high acidity (Okland 1969) and pesticides (Gerhardt et al. 2011). Hence, it can be anticipated that *G. lacustris* will primarily be distributed in

lakes with low anthropogenic pressure. Our results of CAPSCALE analysis show that higher classes of water quality status (lower water quality) characterise mainly lakes inhabited by *C. ischnus*, *D. haemobaphes* and *P. robustoides* (e.g. Lake Śniardwy, Lake Roś, Lake Święcajty), where we did not record *G. lacustris* (apart from Lake Śniardwy in 2009) (Fig. 5).

Instead, we recorded *G. lacustris* in lakes characterised by a high level of shoreline development. Lakes with higher shoreline complexity may provide higher habitat diversity, resulting in lower competition rates between species on environmental resources and, consequently, promoting the possible co-existence of many species, both native and invasive amphipods (Chesson 2000; Amarasekare 2003). While in the lakes with the lower value of this index, native amphipods may be unable to compete with invasive species and could become extinct. However, our results do not confirm this assumption. We found *G. lacustris* in lakes with high shoreline development (e.g. Lake Ełckie), but no invasive amphipods were found there. Isolation of these lakes and low tourist pressure could result in the lack of conditions for their invasion. Nonetheless, in the event of their invasion, we can suppose that the high shoreline complexity of these lakes would promote the co-existence of native and invasive amphipods.

The declining populations of *G. lacustris* in our studies are similar to the general tendency observed in Europe. This species seems to be one of the weakest competitors amongst European freshwater amphipods giving way to the Ponto-Caspian species of genera: *Chaetogammarus*, *Dikerogammarus* and *Pontogammarus* (Meßner and Zettler 2021). *Gammarus lacustris* occurs in a wide range of habitats; nevertheless, in the last few decades, the species has been pushed to the relict range of occurrence (Hesselschwerdt et al. 2008; Meßner and Zettler 2021). Nowadays, the species is present almost exclusively in isolated waterbodies and continues to decline (Meßner and Zettler 2021). The population decline is also attributed to the hydromorphological and hydrochemical changes that occur in aquatic ecosystems (Okland 1969; Matafonov and Bazova 2014).

Similarly, we did not record another native amphipod, *Pallasiola quadrispinosa*, also recorded as declining in the freshwater ecosystems due to invasive amphipods (Żmudziński 1995; Jażdżewski et al. 2004). According to Jażdżewski and Konopacka (1995), this species was found in several lakes of the Masurian Lakeland, i.e. Dargin, Dobskie, Ełckie, Kisajno, Łaśmiady, Mamry, Mikołajskie, Mokre, Niegocin, Śniardwy and Tałty. In some of these lakes, we collected *G. lacustris* without invasive species which suggests also the possible presence of *P. quadrispinosa* in these lakes. *Pallasiola quadrispinosa* thrives in colder temperatures and typically resides in deeper waters during the summer months, which may explain why the species was not recorded during our summer samplings.

Our findings report the set of lake features promoting the distribution of native amphipod species in the studied lakes. As the study area is highly impacted by tourist activities, our results can be useful for better comprehension of the threats to native amphipods in other regions with similar levels of anthropogenic pressure and biological invasions. Our conclusions may highlight the need to protect isolated lakes from tourism and urban area development.

Distribution of invasive amphipods

Freshwater NIS can easily spread with tourist activities, including yachting and angling in particular. Our results show that the number of boats is one of the factors which best explains the distribution of *D. villosus* (Fig. 5). The main part of the Masurian Lakeland with a high abundance of this species covers the area of high tourist activities, i.e. lakes from group I in the northern part of the Lakeland (Figs 2, 4). Yachting is a very significant component of tourism in the Masurian Lakeland, reaching 37% of total tourist activities in the region (Kulczyk et al. 2016). Masurian tourist routes run through these lakes, thus, tourist boat activity supplements yachting. In 2016, we recorded *D. villosus* in all these lakes. A good example is Lake Niegocin, which has a high level of tourist pressure and a rapid invasion of *D. villosus* was observed in 2016. In 2014, the species was absent in this Lake, while in 2016, it constituted 81% of all sampled amphipods. Lake Niegocin is located between the other lakes with high tourist pressure and the Masurian tourist route runs through this lake. The evidence of high tourist activity in this lake can be the high number of car parks per km of shoreline and one of the highest, amongst the Masurian lakes, number of beds in accommodation establishments in 2014 (Kulczyk et al. 2016).

Similar findings were done in other tourist lakes. In Alpine lakes, with higher yachting activity than in the Masurian Lakeland, the expansion of *D. villosus* was caused by yachting and using diving equipment (Bącela-Spychalska et al. 2013; Rewicz et al. 2017). Many species using boat biofouling to invade new waterbodies have broad tolerance to desiccation (Bącela-Spychalska et al. 2013; Glisson et al. 2020). Likewise, *D. villosus* has a high tolerance to air exposure (Rewicz et al. 2014). Moreover, the species is usually associated with another invasive species – zebra mussel (*Dreissena polymorpha*) and can survive up to six days out of the water between mussels fouling the boats (Martens and Grabow 2008). Similarly, the species can be transported with algae and macrophytes (Minchin et al. 2019). It enables them to expand rapidly in new waterbodies, including those isolated from others, by overland transport of boats and yachting equipment.

Overland transport of boats may explain the invasion of *D. villosus* in our study area. Although *D. villosus* was found in most of the recently studied lakes, the species was not found in the River Pisa and the River Węgorapa. These rivers connect the Masurian Lakeland with large rivers, where *D. villosus* is present. It suggests the possible expansion of this species in the Masurian Lakeland by overland transport apart from these rivers. In certain lakes, we did not record *D. villosus*. These lakes have no direct contact with the invaded lakes and low tourist activity almost excludes the possibility of overland boat transport. In contrast to the Alpine lakes, we did not expect diving and angling (using waders) equipment to play a significant role in invading isolated waterbodies by *D. villosus* in the studied area.

Another strong factor explaining the distribution of *D. villosus* is the distance from town. Our results show that this species occurs mainly in the lakes with towns nearby. Proximity to the town and tourist activities are correlated with each other. Most of the marinas are located in towns with well-developed tourist facilities. Indeed, the

proximity to the ports and marinas is an important factor in promoting the expansion of *D. villosus* (Minchin et al. 2019). Higher tourist activities in proximity to urban areas may explain the distribution of *D. villosus* in the study area.

Distribution of other invasive species in the Masurian Lakeland, i.e. *P. robustoides*, *D. haemobaphes* and *C. ischnus*, concerns mainly the lakes with less developed shoreline and rather low water quality (higher class of water status). Predominantly, they are present in lakes with different conditions compared to those where *D. villosus* was found (Figs 4, 5). *Dikerogammarus haemobaphes* is the first Ponto-Caspian invasive amphipod recorded in the Masurian Lakeland (Jażdżewski 2003). This species was recorded in most of the studied lakes, as well as in the Rivers Węgorapa and Pisa. The presence of this species in the Rivers Bug and Narew suggests its invasion in the Masurian Lakeland from the east – from the River Dnieper. Despite the broad distribution of *D. haemobaphes* in the lakeland, this species was quickly over-dominated by *P. robustoides*. The latter species was first recorded in the study area in 2007 (Jażdżewska and Jażdżewski 2008). Three hypothetical routes of *P. robustoides* invasion to this region were proposed – from Kaliningrad (Russia) via the Pregel and the Węgorapa Rivers; from Lithuania via the Augustów Canal; from the Baltic Sea via the River Vistula and its tributaries (Jażdżewska and Jażdżewski 2008). However, since the first record of *D. villosus* in the region in 2014, the abundance of both species – *D. haemobaphes* and *P. robustoides* – drastically decreased until 2016. In 2016, *D. villosus* became the most abundant species in the lakes studied. These results are not surprising as the latter species is a strong competitor and successfully eliminates other invasive and native amphipods (Dick and Platvoet 2000; Platvoet et al. 2007; Bącela-Spychalska et al. 2012; Rewicz et al. 2014; Mathers et al. 2023). Especially, two of them – *D. haemobaphes* and *P. robustoides* – are weaker competitors than *D. villosus*, occurring in different habitats and occupying different niches (Bącela-Spychalska et al. 2012; Kobak et al. 2016; Poznańska-Kakareko et al. 2021; Copilaș-Ciocianu and Sidorov 2022). PCA and CAPSCALE results did not show a strong pattern in the distribution of these species, contrary to *D. villosus*, which suggests that *D. haemobaphes* and *P. robustoides* avoid niches occupied by *D. villosus* (Figs 4, 5). *Dikerogammarus haemobaphes* and *Pontogammarus robustoides* have high desiccation resistance, enabling their overland transport with vessels (Poznańska et al. 2013). Although sailing and angling activities may play an important role in their spreading (Bącela-Spychalska 2016; Csabai et al. 2020), tourist activities probably play a minor role in their distribution in the Masurian Lakeland (Fig. 5).

Another species rapidly spreading in the Masurian Lakeland is *Chaetogammarus ischnus*. In the study area, this species was recorded for the first time in 2014 (Fig. 2A; Suppl. material 1). In two years, its increasing abundance coincided with the decline of the abundance of *D. haemobaphes* and *P. robustoides* (Fig. 2B). In 2016, *C. ischnus* constituted more than half of the collected individuals in Lake Śniardwy. An especially high abundance of this species was observed in the southern group of lakes (group II), contrary to *D. villosus* occurring mainly in the northern group (group I). Moreover, we recorded *Chaetogammarus ischnus* in the River Pisa and did not record this species in the River Węgorapa. These results may suggest that *C. ischnus* invaded the Masurian

Lakeland from the southern direction, i.e. from the River Narew and then via the River Pisa. However, in the lakes where we recorded *D. villosus* and *C. ischnus* co-occurring, the abundance of both species increased. *Chaetogammarus ischnus* usually occupies similar habitats to *D. villosus*, i.e. sites with hard substrate, particularly covered by *D. polymorpha* (Żytkowicz and Kobak 2008; Copilaș-Ciocianu and Sidorov 2022). The co-existence of both species may be attributed to the small body size of *C. ischnus*, which enables this species to occupy microhabitats without interfering with *D. villosus* (Borza et al. 2018). This microhabitat-scale differentiation allows for both species to exist within the same habitat. Between *C. ischnus* and *P. robustoides*, the habitats also overlap, but usually *P. robustoides* limits the occurrence of *C. ischnus* because of its larger body size and more predatory diet (Żytkowicz and Kobak 2008). Therefore, we can hypothesise that *D. villosus* eliminates *P. robustoides* in the lakes studied and then *C. ischnus* refills the empty niche. In several lakes, for example, Dargin and Kisajno, we observed that *C. ischnus* reached a similar abundance in 2016 as *P. robustoides* had in 2014 (Fig. 2B; Suppl. material 1). Similar rapid invasion of *C. ischnus* and elimination of native species was observed in the Great Lakes in the USA (Dermott et al. 1998) and River Rhine in Europe (Van der Velde et al. 2000), where rapid range extension of *D. villosus* was observed as well (Bollache et al. 2004). *Chaetogammarus ischnus* can disperse over great distances (Witt et al. 1997). This species is capable of utilising natural water connections between different water-bodies, but it can also be transported through shipping (Nalepa et al. 2001). Witt et al. (1997) noted that the euryhaline nature of the species enables it to be transported even via ballast waters. However, the understanding of the invasion process of *C. ischnus* is limited and demands further studies.

Our results constitute an important contribution to the long-term observation of expansion dynamics of Ponto-Caspian amphipods and can be part of global databases monitoring invasive species. Rapid expansions underline the importance of regular, annual samplings in lakes and watersheds connecting them with invasion corridors. We show the very important role of tourist activities in lakes in the expansion of alien amphipods, in particular of *D. villosus*. These findings underline the important role of permanent monitoring of yachting and shipping vessels. Our predictions can be applicable in other tourist freshwater areas and help designate protection zones limiting boating. Our results can be also valuable to studies on other biofouling taxa. The significance of the town's proximity for the amphipod invasion is due to well-developed tourist facilities in urban areas and possibly water pollution; thus, lakes shorelines and marinas should be controlled as well. Water connections between lakes also should be regularly monitored. Our records of *Chelicorophium curvispinum* in the River Narew in 2014 and 2016 suggest that this species may be the next recorded invasive amphipod in the Masurian Lakeland (see Suppl. material 1). Some studies show a rapid expansion of *C. curvispinum* in freshwater ecosystems with the presence of *Dreissena polymorpha* and shipping (Van den Brink et al. 1993; Jażdżewski and Konopacka 2002). The current distribution of other invasive amphipods, for example, *Obesogammarus crassus* and *Gammarus tigrinus*, suggest no direct risk of their expansion in the Masurian Lakeland soon, but permanent monitoring of their expansion is necessary.

Limitations of our study

Although our data come from several years, it is important to indicate that the most recent data come from 2016; thus, the current invasion status in the study area can be worse than what we present here. The lack of lakes where native and invasive amphipods co-occur makes some of our findings difficult to interpret and partially speculative.

One of the crucial findings of our study is the impact of boating on the invasions. However, we need to remember that the methods we used have some limitations. We used the maximum capacity of marinas as the number of boats in use. Although on busy days the percentage of used boats in the total number of moored boats is high, as shown in Ros et al. (2013), these data are not precise and might be an under-representation of reality. We need to remember that, the association between boat density and the propagation of invasive amphipods has not been established through direct observation of vessel biofouling communities.

Lakes, especially those with high shoreline complexity, provide many habitats which various species can occupy. Therefore, analysing the data based on one sampling per lake may not depict the real diversity of the amphipod communities. Especially, the lack of records of amphipods in Lake Nidzkie, which has a connection with other lakes and Masurian tourist routes, suggests not enough efficient sampling. We need to be aware that the absence of a species in one sample does not exclude the possible occurrence of this species in other habitats of the same lake. Thus, our results, showing the replacement of native species by invasive species, present interesting trends, but are insufficient to conclude the extinction of certain species. Therefore, our findings should be perceived as predictions, not postulates.

Future directions

Future studies would benefit from utilising a more thorough and systematic sampling to provide a more accurate and reliable picture of the invasion process.

Our results show the importance of the proximity of sampling points to towns for invasions. Although we assume that this correlation is connected with tourist facilities and pollution, implementation of more data is needed in the future. Particularly, the distance between sampling points or lake centroid and marinas should be implemented in the analyses (Cole et al. 2019; Minchin et al. 2019). A significant effect of distance to marinas on invasions was noted by Minchin et al. (2019). Marinas are critical entry points for many invasive species and may play the role of reservoirs for newly-introduced invaders (Glasby et al. 2007; Ros et al. 2013; Fernández-Rodríguez et al. 2022).

Additionally, using the actual number of boats in use in the area would be advisable as was done in studies by Bącela-Spychalska et al. (2013) and Keramidas et al. (2018). Moreover, our knowledge about what part of the vessels are fouled by amphipods, which particular species can be transported and on what maximum distance is still scarce. Future studies would also benefit from including inspections of boats and ropes to identify potential vectors for amphipods, such as algae and mussels.

Dikerogammarus villosus, *Chaetogammarus ischnus* and *Chelicorophium curvispinum* can be transported with zebra mussels. Therefore, it is advisable to incorporate data on the occurrence of *D. polymorpha* in lakes and on vessels for future research. The type of vessel can also be an important factor. For instance, motorboats can be vectors of invasions, while canoeing does not play this role (Venohr et al. 2018). In this context, the presence/absence of silent zones, i.e. lakes or their parts where using boats with motors is forbidden, should complete the analyses. Knowledge about the success of the "check, clean and dry" strategy in the study area is missing. We expect that none of these methods is implemented as the local law does not demand their respecting. The method to prevent transporting invasive species on boats, as described in Mohit et al. (2021), should be tested in the Masurian Lakeland. Surveys amongst fishermen and tourists are worth collecting and analysing (Cole et al. 2019). To gain deeper insights into these dynamics, we recommend the establishment of an inter-lakes traffic registry. This registry would provide crucial data regarding boat traffic and potential pathways for the introduction of invasive species. Prevention measures and facilities for anglers should also be studied (Smith et al. 2023). To better understand which species can be transported by vessels, it is important to experimentally test the resistance of different invasive species like *C. ischnus* and *C. curvispinum* to desiccation.

As far as the financial and technical situation allows, samples should be collected from a large number of points on each lake. Additionally, studying a greater set-up of lakes would allow better tracking of invasions and more accurate detection of all amphipod species in the lakes. Finally, tracking of the invasion process can be supported by molecular studies (e.g. Mamos et al. (2021)).

Conclusions

The rapid expansion of the invasive Ponto-Caspian amphipods observed in this study aligns with a general trend along European freshwater basins. The contraction of the range and niche of native species when faced with more aggressive (e.g. *D. villosus*) and/or generalist (e.g. *C. ischnus*) species is something expected and confirmed by our findings. Even though many lakes seem to be still free from amphipod invaders, this may be for a short time considering the abrupt increase we have registered in just two years.

Our study emphasises the need for a comprehensive approach to understanding and addressing the dispersal of alien species through human activity. Our findings highlight the important role of boats in the spread of invasive amphipods within lake systems. The invasion process of *Dikerogammarus villosus* especially suggests the possible impact of overland boat transport in spreading this species in new lakes.

Furthermore, it is essential to raise awareness amongst lake users about the negative consequences of biological invasions and the necessity of implementing a "check, clean and dry" policy. By educating and engaging lake users, we can foster a sense of responsibility and cooperation in preventing the spread of invasive species. Implementing these measures collectively will contribute to better biosecurity practices and safeguard the ecological integrity of lakes against invasive species.

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Supplementary material 1

Metadata for each sampling site and date

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Data type: xlsx

Explanation note: Sampling sites between the years 2001–2016 with a number of individuals (or +/-) for the presence/absence) of each recorded Amphipoda species (names of invasive species have been underlined). Symbols for lakes provide two-letter acronyms used on the figures. Symbols for rivers and canals provide three-letter acronyms used on the figures. Water QS: Water quality status (Soszka et al. 2016); A/V ratio: Surface area to volume ratio (Soszka et al. 2016); Shoreline development: Shoreline length to surface area ratio (https://mojemazury.pl); Density of boats: number of boats per ha of lake surface (https://mazury24.eu; https://skorupki.mazury.info.pl).

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Supplementary material 2

Summary of the best-fitting Bernoulli GLMM for the presence of native gammarid – *Gammarus lacustris*

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Data type: docx

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Link: https://doi.org/10.3897/neobiota.90.109221.suppl2

Supplementary material 3

Results of PERMANCOVA test using 9999 permutations

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Data type: docx

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Link: https://doi.org/10.3897/neobiota.90.109221.suppl3

Supplementary material 4

Supplementary image

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Data type: jpeg

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